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identified by the large number of white feathers. She has been divorced for the past ten years and is apparently living a single life.

Many other species and pairs could be cited, but as yet we have only circumstantial evidence on which to base the conclusions set forth in the first paragraph.

Escondido, California, November 15, 1918.

PARASITISM OF NESTLING BIRDS BY FLY LARVAE

By O. E. PLATH

URING the summer of 1913, while studying bird life in and about Berkeley, California, I fed up some fifty to sixty wild-taken nestlings which included the following species: California Purple Finch (Carpodacus purpureus californicus), California Linnet (Carpodacus mexicanus frontalis), Willow Goldfinch (Astragalinus tristis salicamans), Green-backed or Arkansas Goldfinch (Astragalinus psaltria hesperophilus), Lawrence Goldfinch (Astragalinus lawrencei), and Lazuli Bunting (Passerina amoena). In most instances these nestlings were taken a few days before they were full-fledged, together with nest and surrounding branches. Before being taught to eat by themselves, they were fed by means of a curved stick in bird fashion, that is to say not forcibly, but by making them realize that they could get food from the beak-shaped end of the stick as they did formerly from the beaks of their parents. This method of feeding usually extended over a period of from several hours to several days, depending upon the age and intelligence of the nestlings.

After having succeeded in feeding up several broods without loss, I attempted to rear a nest of five Green-backed Goldfinches, but despite the fact that all five ate readily from the stick, all but one died in a few days. On taking this nest of goldfinches, I had noticed that two or three of the nestlings had swollen eyelids, in some cases swollen to such an extent that it was impossible for the nestlings to open their eyes. Just previous to this time I had contracted a severe case of oak poisoning while roaming through the underbrush in the canyons and along the creeks, and thought that perhaps the nestlings might be afflicted with the same malady. While feeding them, I had noticed furthermore that their mouths were considerably paler than those of the birds which had been fed up previously. They also appeared less vigorous and did not exhibit the same ravenous appetite which healthy nestlings show. Their mouths became paler and paler and within two or three days four of the nestlings died, as I have already mentioned, and even the remaining one looked as though it would not live long. order to keep it warm, I removed it from the nest and placed it in some warm woolen cloth. To my surprise I noticed a number of maggots, similar in size and form to bumble-bee larvae (about 1.5 cm. in length and 0.5 cm. in width), crawling about in the nest. Upon picking the latter apart, I found some twenty or thirty of these maggots. They were creamy white in color and the anterior end of the alimentary canal of a number of them contained a bright red substance which changed to a blackish brown color in the posterior part of the intestinal tract. The other maggets contained the same blackish brown substance, but not the red.

The pale mouths and ultimate death of the nestlings were no longer a mystery. They had been gradually bled to death by the maggots. I regretted the unhappy fate of the young songsters and avenged them as best I could by killing the maggots, thinking that this form of parasitism was no doubt generally known to zoölogists. The surviving nestling soon recuperated and later became a great pet of the family.

Intermingled with the lower part of this infested nest there was a mass of a sticky, dark brown substance reminding one of clotted blood. Evidently this material either was the faeces of the maggots or coagulated blood which had trickled from the wounds made by the maggots, but as I could find no trace of wounds on the birds, I concluded it to be the former.

About two weeks later I found the nest of a Willow Goldfinch containing four young ones, some of which showed the same symptoms as the Green-backed Goldfinches which had died. Suspecting that this nest also might be infested by maggots, I transferred the four nestlings to another nest and closely examined their own nest. I found the same state of affairs as in the previous infested nest, with the exception that some of the maggots had already pupated. These pupae were of a light brown color and somewhat smaller than the maggots, being about 1.0 cm. in length and 0.5 cm. in width. Both maggots and pupae were destroyed as in the first case. The swelling of the eyelids soon disappeared and I had no difficulty in rearing this brood of goldfinches; but one of the young birds turned out to be entirely blind so that it had to be killed. Two others were blind in one eye, whereas the fourth was normal. Two of these birds lived in captivity for several years.

Later in the summer I met Dr. C. A. Kofoid, head of the Zoölogical Department of the University of California, and told him about the maggots and the pupae. He regretted that I had destroyed them and suggested that I look into this matter more closely the following summer. It was impossible for me to do this, however, until the summer of 1917. The period of investigation which I am now about to discuss, extended from the latter part of June, 1917, until about the middle of September. The work was carried out under the supervision of Professor W. W. Cort, of the Department of Zoology of the University of California, to whom I am indebted for a number of important suggestions.

My first task was to see whether or not I could find any maggots. Since both infested nests had been those of goldfinches, I tried to locate as many of these nests as possible. Incidentally I also kept an eye on nests of other birds which I chanced to run across. My efforts were quickly rewarded. The first nest examined, that of a Nuttall Sparrow (Zonotrichia leucophrys nuttalli), contained thirty-six full-grown maggots like those encountered in the summer of 1913, and thereafter I found them in about two out of every three nests.

To my surprise none of the young birds from these infested nests showed any eye trouble; nor did they, in the first few instances, seem to have fared any the worse in other respects from the presence of the maggots. Equally surprising was the fact that no red appeared in any of the maggots taken from the first few nests, but merely the dark brown substance in the posterior part of the intestine. Ninety of the most vigorous maggots, selected from 154 full-grown individuals taken from the nest of a California Linnet, whose five full-fledged young showed no noticeable pernicious effects from this large number of creeping vermin, were placed in a Green-backed Goldfinch nest containing three young which were about four or five days old, and developments observed from day to day.

One of the nestlings died about two days later. Though it seemed plausible that death had been caused by the maggots, a post-mortem examination furnished no absolute proof for this assumption. The other two nestlings seemed to be considerably retarded in their growth, but finally left the nest. After the departure of the young, only forty-three of the ninety maggots were recovered from the nest, some of them in the form of pupae, showing that many of them had evidently lost their bearings and fallen out of the nest. None of them showed any trace of red. These facts made my former conclusions, that these maggots were blood-sucking parasites, appear doubtful.

About this time I was observing two California Linnet nestlings. Despite the fact that there were only two young instead of from three to five, as is usually the case, I noticed that they were growing very slowly and that they lacked the same vigor and liveliness usually exhibited by this species of bird. When I finally succeeded in getting them to take wing, I obtained fifty-four maggots from their nest, many of which showed the sought-for red substance similar to that observed in 1913. These maggots were only about two-thirds the size of those taken from the first few nests, but to all appearances belonged to the same species.

At the laboratory several of the maggots with the red substance in them were decapitated and smears made from this red material which was then examined under a high power microscope. The red substance proved to be fresh vertebrate blood which of course could only have been obtained from the birds inhabiting the nest. But in order to prove this beyond a doubt, a number of additional experiments were carried out.

A few days later I obtained twenty exceedingly small maggots from a California Linnet nest just vacated by its feathery occupants. Although only about one-fourth grown, every one of them showed traces of fresh blood. All twenty were placed in the nest of a Green-backed Goldfinch containing three young about ten days old and the latter observed from day to day. Nothing extraordinary happened, excepting that the three nestlings seemed to be rather weak when they left the nest about two weeks later. When the nest was picked apart, all twenty maggots were recovered. They had meanwhile reached full growth. None of them however showed any trace of blood, but merely the usual dark brown substance in the posterior end of the intestine. These facts tend to indicate that the maggots are voracious feeders during the earlier period of their existence, but that they refrain from taking food after they have attained full growth.

As probable as it seemed that the vertebrate blood found in the maggots was avian blood obtained from the nestlings, this had not yet been absolutely proved, since I had never seen any of the maggots attached to the nestlings. Moreover my experiments up to that time, due to the difficulty of closely observing nestlings of wild birds in the open, had naturally been somewhat superficial. In order to remedy this difficulty, I decided to use a brood of tame canaries for subsequent experiments. I succeeded in securing a female bird with two nestlings about a week old, but both young died within a few days, probably because they had taken cold while being transferred to my room. For these I substituted four, nearly full-fledged Green-backed Goldfinches. The old bird seemed to notice the deception, but when she saw the four open, hungry mouths, she adopted the strangers as her own. A few days later I selected from some 200 maggots, forty of the most active ones and placed them on the young birds. The maggots

had been without food for a number of days and many of them were only half grown.

At first the nestlings showed some uneasiness by shaking themselves, but this only lasted for a minute or two, after which they again came to complete rest. They were observed from time to time until about 8:30 in the evening, but there was nothing unusual in their behavior. At about three o'clock the next morning I was suddenly awakened by a thud in the cage. My first thought was that the mother bird had become frightened and had jumped from the nest; but when I looked, I found one of the nestlings down below. I was still more surprised to see the others, including the old bird, sitting on the rim of the nest and not huddled closely together in the center. When I picked up the nestling which had leaped down. I noticed two maggets crawling about at the bottom of the cage, but upon examination found no maggets on the bird itself. The two maggots which had been dragged down by the nestling—it being impossible for them to get out of the nest-box in any other way—were not full-grown and were gorged with blood. Thereupon the four remaining birds were carefully examined.

I now saw what I had been expecting to see: A number of maggets were clinging to the feet and lower parts of the body of each one of the nestlings. None were found on the mother bird. Most of these maggets released their hold while the birds were being examined, but some of them had to be forcibly detached. These, like those found at the bottom of the cage, were not full-grown but were filled with fresh blood. No marks, visible to the naked eye, could be seen where the maggets had pierced the skin of the birds, nor were any traces of blood apparent. This was conclusive proof that the sticky material found at the bottom of infested nests is not coagulated blood which has dripped from the wounds made by the maggots, but faeces deposited by the latter. The four nestlings were then transferred to another nest and their own carefully examined. Sixty-eight maggets were taken from the nest, showing that the nest had originally harbored twenty-eight. More than half of the sixty-eight maggets showed traces of fresh blood, the smaller ones being most gorged. The soft cotton lining of the nest-box was then removed and carefully examined, but no additional maggots were discovered. Thereupon the box was refilled with cotton and the nestlings put back. The latter now appeared completely at ease. They again huddled closely together as formerly, the mother bird sitting on them during the night.

During the next few days a number of other experiments were carried out with this brood of goldfinches. While one of them was being held in the hand a few vigorous, half-grown maggots were placed among the nestling's feathers. After crawling about among them for a brief period, the maggots would invariably drop from the bird. One evening several dozen half-grown, hungry maggots were placed in a pasteboard box and covered with a layer of soft cotton about an inch thick. Two of the nestlings were then transferred to this box and the latter covered up. In less than ten minutes eight or nine of the maggots were found firmly attached to the nestlings, ingesting blood, only a few releasing their hold while the birds were being examined. This same experiment was tried the following afternoon, but, strange to say, none of the maggots were attached to the birds. But when this experiment was repeated the same evening, and on subsequent evenings, some maggots were again found clinging to the nestlings. This indicates that they do their deadly work at night and rest in the lower parts of the nest during the day. It is interesting to note that both of the nestlings which

were used for these experiments died several days later, apparently from loss of blood.

During the eleven weeks over which this investigation extended, the maggots and the resulting flies, since identified as the larvae and adults of *Protocalliphora azurea* (Fallen) by Mr. C. W. Johnson, curator of the Boston Society of Natural History, were studied carefully. These larvae were kept in pasteboard boxes, in some of which soft cotton or bird nest material was placed. They crawled about vigorously until they reached a dark place, the crevices between the layers of paper of the boxes being their favorite resting place.

In these pasteboard boxes various organic substances were placed, such as fruit, bread, meat, and boiled potato. Although the fly larvae crawled through some of these substances, they fed upon none of them. One day I secured a large bone containing many blood cavities. Among these blood cavities I bored several holes with my penknife and placed the bone in a box containing several dozen fly larvae. The latter had been starved for about a week so that there was not the slightest trace of food left in their intestines. The next morning $\bar{1}$ found two or three of them with fresh traces of blood in their alimentary canals, conclusive evidence that they had been feeding upon the ox blood contained in the bone. One day, having accidentally cut myself, I put several drops of blood in the palm of my hand and placed several larvae near it, but the latter invariably crawled in the opposite direction as soon as they came in contact with the blood. Similar experiments with ox blood brought the same results. This seems to indicate that the larvae require a firm object to which they can attach themselves before they make any attempt to ingest blood.

Larvae which had not reached their full growth when taken from nests invariably died, unless they could feed upon blood. On the other hand full-grown larvae always pupated, even if they had no access to food of any kind. This shows that the larvae of *Protocalliphora azurea* are absolutely dependent upon blood in order to mature.

The blood ingested by the larvae is stored in a kind of reservoir, the diverticulum, which branches off from the esophagus close behind the pharynx and there retains its red color for three or four days, gradually passing into the posterior end of the intestine as a dark brown substance which appears as a longitudinal streak in the middle of the animal's body. If the larvae are not fed, this streak is gradually discharged as faeces so that after five to seven days more, the larvae become creamy white in color throughout. From this we may infer that it is not necessary for the larvae to replenish their supply of food at frequent intervals to attain full growth.

When the larvae are about to pupate, they crawl, anterior end downward, into the sticky mass at the bottom of the nest and there sometimes form a kind of disk, the lower side of which is made up of the anterior ends of the larvae, and the upper side of the posterior ends. About two weeks after pupation, the young flies emerge from the lower side of the disk. The whole thing reminds one somewhat of the state of affairs in wasp nests. Here too the young wasps emerge from the lower side of the disks. In captivity the fly larvae, before they pupate, usually attach themselves to objects located in dark places by means of a viscous fluid which solidifies a few moments after it has been discharged.

One thing which surprised me very much was the power of resistance which these larvae showed. Several of them, after having been immersed in a 70 percent alcohol solution for twenty-four hours, were still wriggling vigorously. Sev-

eral others which were being prepared for dissection were placed in a fixing fluid for six hours, then washed in a 50 percent alcohol solution and placed in one of 80 percent. They were still alive two days later and it was necessary to resort to a stronger fixing fluid (Gilson's) to prepare them for dissection. Other larvae were placed in a very strong insect powder, but they remained alive in it for two or three days.

As soon as the larvae pupated, the pupae were placed beneath inverted tumblers. After the flies emerged from the pupae they were kept in a large, narrow-mesh cage and carefully studied. It may be of interest to state that the flies (about 1500), practically without exception, emerged from the pupae between seven o'clock in the morning and two o'clock in the afternoon. Upon emerging they were of a slightly lighter hue than the adult of our Common House-fly (Musca domestica), their wings being shriveled up, but after about an hour or so these straightened out and the young flies assumed the dark blue, metallic lustre of adult Protocalliphora azurea.

Various kinds of food were placed before these flies, such as milk, crushed fruit, cheese, and meat in various forms. The flies readily ate the milk and fruit, especially if the latter was placed on the cage wire instead of the cage floor, but they were rather indifferent to the meat and the cheese. Although some of the flies were kept in the cage for six or seven weeks, none of them, to my knowledge, deposited eggs or maggots.

One day I noticed a number of very small, bee-like insects, since identified as Nasonia brevicornis by Professor Brues of Harvard University, flitting about in one of the inverted tumblers. I wondered where they had come from, but thinking that they had perhaps got into the tumbler accidentally, I let them escape. To my surprise I found some twenty or thirty more of them under the same tumbler the following day. Upon investigation, I found one or two small holes of about the size made by an ordinary stick-pin in several of the pupae. I could easily tell by the weight of the latter that they were empty. This gave me a clue. I opened a number of the pupae and there found these little insects, more commonly known as Chalcid Flies, in several stages of development: as white, inactive maggots; as creamy, pink-eyed larvae, already showing their insect form; and as full-grown insects which came swarming out as soon as the fly pupae were opened. I counted the Chalcid Fly larvae from a dozen pupae and found them to vary in number from about fifteen to twenty-five per Muscid pupa. In all these cases the embryo fly had been completely devoured.

Some forty or fifty of these Chalcid Flies were then transferred to an inverted aquarium jar below which a hundred Muscid pupae were placed. The Chalcid Flies seemed to be perfectly at home among these pupae, crawling about among them as do bumble-bees among their honey-combs. Within a few weeks hundreds upon hundreds of young Chalcid Flies emerged from the Muscid pupae; less than a dozen *Protocalliphora* hatched, the remaining ones having been parasitized by the *Nasonia*.

In some of the infested birds' nests, I had noticed a number of small grubs, similar in size and form to those found in almonds. As in the case of the Chalcid Flies and the larvae of the *Protocalliphora*, I paid no attention to them at the beginning, but when they occurred repeatedly, I began to suspect that they might have some relation to one or both of the other insects. I therefore collected some fifty or sixty of these grubs and placed them among a large number of Muscid pupae, many of which were parasitized by Chalcid Flies, and watched

developments from day to day. I found that these grubs fed upon the pupae, eating shell and all, and apparently being quite indifferent as to whether the pupae contained Chalcid Fly or Muscid larvae.

From these grubs several species of moths hatched. A few living specimens of these moths were turned over to Professor Wheeler of the Bussey Institution for identification, together with some Nasonia brevicornis and Protocalliphora azurea. It was necessary to send the moths to the United States Bureau of Entomology at Washington, where they were partially identified by Mr. Carl Heinrich. Among them were two species of Tinea, one of which was definitely identified as Tinea occidentella (Chambers). There was only one specimen of the other species and that was too badly rubbed for specific determination. A specimen of another species proved to be an Oecophorid, probably Endrosis lacteella (D. & S.), or a closely related species, but also too badly rubbed for exact identification. Several of these moths were retained for the United States entomological collection by the entomologists at Washington.

It will now perhaps be of interest to ornithologists and entomologists, as well as to bird lovers in general, to state how frequently the larvae of Protocalliphora azurea were encountered in birds' nests and what effect their bloodsucking habit has on the nestlings. During the eleven weeks in which these experiments were carried on, no less than sixty-three nests, representing six species of birds, were examined. Of these, thirty-nine, or nearly two-thirds, were infested by blood-sucking fly larvae. The following tables will help to illustrate.

TABLE I					
Species of bird	1	Nests exam- ined	Infested nests	nests	of
Nuttall Sparrow		4	4	0	infestation 100
California Purple Finch and California		•	•	v	100
net		31	21	10	67
Green-backed Goldfinch		13	8	5	61
Willow Goldfinch		7	4	3	57
California Brown Towhee		8	2	6	25
Totals		63	39	24	61
					(Average)
TABLE II					
Species of bird		Larvae in		Totals	Larvae
California Purple Finch and California	Lin.	each nest			per nest
net		8, 10, 14, 1	5.		
100	•••••	17. 20. 23. 2	•		
		50, 52, 54, 6	•		
		62, 71*, 80			
		94, 103, 10	3,		
		106, 108, 1	54.	1239	59
California Brown Towhee		44, 6	2.	106	53
Willow Goldfinch				152	38
Nuttall Sparrow				133	33
Green-backed Goldfinch				014	0.0
m		28, 30, 35, 5	0.	214	26
Totals				1844	47

*A considerably smaller, but apparently more deadly species than Protocalliphora azurea (Fallen).

47 (Average)

From the first table it will be noticed that birds which build a rather compact nest, for example the goldfinches and the linnets, show a considerably larger proportion of infection than those which construct nests of a looser texture, as for instance the California Brown Towhee. This may possibly be due to the fact that it is difficult for the fly larvae to keep from falling out of loosely constructed nests.

All of the 1844 larvae in Table II, excepting the seventy-one indicated by the starred foot-note, were those of *Protocalliphora azurea*. These seventy-one larvae were taken from a linnet nest which contained the skeletons of three young which had been overtaken by death just before they became full-fledged. Death had undoubtedly been caused by the larvae. When the latter were discovered, they were in their pupal stage and were considerably smaller than the larvae of *Protocalliphora azurea*. All of them, excepting about a dozen, had hatched. These unhatched pupae were guarded very carefully, but they all proved to be parasitized by *Nasonia brevicornia*.

The death of six other nestlings, including the four which had died in 1913, could be traced with more or less certainty to the Muscid larvac, as in the case of the three linnets whose skeletons I found, and the two goldfinches used for experimenting. One of these nestlings, a nearly full-fledged California Linnet, was discovered when it had been dead only a short time. A number of the *Protocalliphora* larvae had actually penetrated into its body. The nest in which this dead bird was found contained another nestling of the same brood. Though apparently rather weak, this nestling took wing when I approached the nest. Nearly all of the fly larvae found in this nest showed traces of fresh blood.

It was not until after I had completed my investigations that my attention was called to two articles concerning blood-sucking fly larvae¹. As far as I am able to ascertain, these are the only two instances of blood-sucking fly larvae on record as far as North America is concerned. In the second of these two articles Coutant mentions four papers (those by Dufour, Du Buysson, Rouband, and Rodhain) concerning blood-sucking fly larvae in Africa, South America, and Europe, but neither the Harvard University Library nor the Boston Public Library contain any of these four articles.

In 1908 Henshaw (loc. cit.) recorded the infestation of two successive broads of Bluebirds (Sialia sialis) by the larvae of Protocalliphora chrysorrhea (Meigen), which had been reported to him by Mrs. Emma F. Everett, of Wellesley Hills, Massachusetts. These two cases of parasitism were decidedly fatal, seven out of the eight nestlings dying as a result. Henshaw closes with a note of warning about the danger of this insect pest to our native birds.

Seven years later Coutant (loc. cit.), while studying blood parasites of the Common Crow (Corvus brachyrhynchos) at the Biological Laboratory of Cornell University, came across some larvae of Protocalliphora azurea. Most of his deductions, based upon the study of these larvae, are well founded. His conclusion however (loc. cit., p. 139) that "the larvae prefer rather dry places to moist ones and are therefore not accustomed to living in decomposing or fecal material" and that (loc. cit., p. 143) "the larvae when ready to transform, apparently leave the more occupied parts of the nest in the vicinity of their food-supply and seek a dry . . . portion" of the nest, were not borne out by my observations and experiments. In all cases the larvae preferred the moist faecal material and pupated in it. This discrepancy between Mr. Coutant's results and mine is undoubtedly due to the fact that Mr. Coutant based his conclusions upon the study of a comparatively few larvae, and that even these few were not studied by him in their natural environment, the bird's nest.

¹a. Henshaw, H. W. A Parasitic Fly Injurious to our Native Birds. The Auk, xxv, 1908, pp. 87-88. b. Coutant, Albert F. The Habits, Life History, and Structure of a Blood-sucking Muscid Larvae (*Protocalliphora Azurea*). Journal of Parasitology, vol. I, 1915, pp. 135-150.

Commenting upon the fact that Protocalliphora azurea is recorded by collectors and dipterologists as "rare" or "very rare" and that specimens of this fly are only to be found in the larger museums and collections, Coutant correctly assumes (loc. cit., pp. 144, 145) "that they are not so rare as is generally supposed, but that the adults are peculiar in their habits, flight, etc., and for this reason are rarely taken". He then goes on to say (loc. cit., p. 145): "Few collectors, I imagine, have taken insects very often from the zone of air from fifty to one hundred feet above the ground, in the woods; yet from the habits of the larvae, this is where we would naturally expect that the adults would occur". This is probably correct, but the lower limit, as well as the lateral, will have to be extended considerably. Most of the thirty-nine infested nests taken during the course of my experiments, as well as the two encountered in 1913, were found far distant from forests and all of them came from a height of three to fifteen feet above the ground.

Turning now to the effect which these blood-sucking larvae of *Protocalliphora azurea* have on nestling birds, my observations seem to warrant the following conclusions: (1) that from 5 to 10 percent of the parasitized nestlings dic from loss of blood; (2) that some of the parasitized nestlings which do become full-fledged are so weakened by the loss of blood that they fall an easy prey to rapacious animals; (3) that the larvae of *Protocalliphora chrysorrhea* are probably more deadly to nestling birds than those of *Protocalliphora azurea*. The last conclusion seems to be borne out by the case of parasitism recorded by Henshaw (*loc. cit.*, pp. 87-88), where there was a fatality of nearly 90 percent instead of one of only 5 to 10 percent.

Much remains to be done along this line of investigation in order to determine how large and universal the damage is which is wrought on our continent by this insect pest. Although the adults of both Protocalliphora azurea and Protocalliphora chrysorrhea are very rarely taken by collectors (cf. Henshaw, loc. cit., p. 88; Coutant, loc. cit., pp. 144-145), my investigations prove conclusively that the former is not so rare, at least not in certain parts of the country. So far, however, only forty-four birds' nests, infested by the larvae of one or the other of these flies, have been recorded. All forty-four of these infested nests were found at three places, one near Ithaca, N. Y. (Coutant, loc. cit.), two at Wellesley Hills, Mass. (Henshaw, loc. cit.), and the remaining forty-one in the San Francisco Bay region. It would be highly interesting, and perhaps for the benefit of our wild birds, if bird students in other parts of the United States, as well as in Canada and Mexico, would thoroughly investigate this matter in their home districts.

Massachusetts Institute of Technology, Cambridge, Massachusetts, May 7, 1918.